Arch. Hydrobiol. Spec. Issues Advanc. Limnol. **58**, p. 175–199, August 2003
Lake Stechlin

Deep layer cyanoprokaryota maxima in temperate and tropical lakes

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with 9 figures and 3 tables

Abstract: Deep layer cyanoprokaryota *(Cyanobium, Planktothrix rubescens, Cilindrospermopsis raciborskii,* mixed assemblage*)* maxima were observed in Lake Stechlin (Mecklenburger Lake District, Germany) and in Lake Dom Helvécio and Lake Carioca (Rio Doce Lake District, Brazil). All three of these lakes have trophic states between oligotrophic and mesotrophic and the euphotic depth exceeds the mixing depth in each case. In terms of density gradient stratification, tropical and temperate lakes are in a similar range and the position of the deep chlorophyll maximum (DCM) in upper hypolimnion. At the level of DCM light intensities of about 1% of subsurface irradiation are characteristic and can suffice the light demand of shade adapted species. Availability of phosphate-P was higher in the hypolimnia of the investigated lakes, therefore this can be a selective advantage for DCM populations. Although upper hypolimnia are rather stable habitats that, in theory, would allow the best adapted species to exclude all others, cyanoprokaryotic DCM can be bi- or multispecific. In multispecific DCM, weather-driven irregularities in the stability of the pycnocline might maintain a multispecific DCM assemblage. Co-dominance of *Cyanobium* and *Planktothrix* in Lake Stechlin probably exhibited a stable co-existence when one of the species was limited by light and the other by the availability of P. Occurrence of DCM by buoyant cyanoprokaryota is probably much more common in lakes of moderate (from ultra-oligortophy to moderate mesotrophy) trophic state independent of latitudinal differences and they may play a key role in matter and energy cycling of freshwater.

Key words: *Cyanobium, Planktothrix rubescens, Cylindrospermopis raciborskii,* DCM, deep lakes

Introduction

Apart from the well known deep-layer density maxima of *Planktothrix (Oscillatoria) rubescens* (KONOPKA 1982, FEULLIADE et al. 1984), records on deep chlorophyll maxima (DCM) have accumulated during the last 30 years. A selection of species described in DCM of freshwater lakes (Table 1) shows a high diversity of species or groups of species involved and implies that reasons for development DCM are also diverse.

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1612-166X/03/0058-0175 $ 6.25

The deepest DCM reported from freshwater environments occur in the clearest ultra-oligotrophic lakes. In Lake Tahoe, summer chlorophyll maxima occur at 100 m partly due

Table 1. Species contributing to deep-layer chlorophyll maxima in freshwaters. Group abbreviations: Cya – Cyanoprokaryota, Cry – Cryptophyta, Dino – Dinophyta, Chryso – Chrysophyceae, Xantho – Xanthophyceae, Prim – Prymnesiophyceae, Centr – Centrales, Chloro – Chlorophyta.

species	group	Reference
Planktothrix agardhii	Cya	EDMONDSON (1970), KLEMER (1976), LINDHOLM (1992), KONOPKA et al. (1993)
P. rubescens	Cya	KONOPKA (1982), FEULLIADE et al. (1984)
Lyngbya limnetica	Cya	REYNOLDS et al. (1983)
Planktothrix sp.	Cya	GERVAIS (2000)
Lymnothrix rosea	Cya	MEFFERT (1989)
Aphanizomenon flos-aquae	Cya	KONOPKA (1989)
Anabaena sp.	Cya	KONOPKA (1989)
Cylindrospermopsis raciborskii	Cya	BARBOSA & PADISÁK (in press)
Synechococcus sp.	Cya	STEENBERGEN & KORTHALS (1982), CRAIG (1987), WEISSE & KENTER (1991), CALLIERI & PINOLINI (1995)
Cyanobium sp.	Cya	PADISÁK et al. (1997)
Cryptomonas phaseolus	Cry	PEDRÓS-ALIÓ et al. (1987), MIRACLE et al. (1992)
C. erosa	Cry	MIRACLE et al. (1992)
C. obovata	Cry	MIRACLE et al. (1992)
Trachelomonas hispida	Eug	MIRACLE et al. (1992)
Euglena spp.	Eug	MIRACLE et al. (1992)
Ceratium hirundinella	Dino	GÁLVEZ et al. (1988), KONOPKA (1989), GERVAIS (2000)
Dinobryon sertularia	Chryso	BIRD & KALFF (1989)
Ochromonas sp.	Chryso	BIRD & KALFF (1989)
Chrysosphaerella longispina	Chryso	PICK et al. (1984)
Mallomonas caudata	Chryso	STEENBERGEN & KORTHALS (1982)
Tribonema sp.	Xantho	LARSON et al. (1987)
Scourfieldia caeca	Prym	CROOME & TYLER (1984)
Dinobryon bavaricum, Synedra ulna, Cyclotella striata, C. comta	various groups	ABBOTT et al. (1984)
Urosolenia eriensis	Centr	JACKSON et al. (1989)
Cyclotella spp.	Centr	JACKSON et al. (1989)
Urosolenia eriensis, Cyclotella kuetzingiana, C. stelligera, C, radiosa, C. ocellata	Centr.	SHORTREED & STOCKNER (1990)
Stephanodiscus hantzschii	Centr	LARSON et al. (1987)
Dinobryon sp., *Synedra* sp., *Tabellaria* sp., *Oocystis* sp., *Chlorella* sp.	various groups	GROSS et al. (1997)
Astasia sp.	Chloro	MIRACLE et al. (1992)
Crucigenia tetrapedia	Chloro	GASOL & PEDRÓS-ALIÓ (1991)
Selenastrum capricornutum	Chloro	GASOL & PEDRÓS-ALIÓ (1991)

to sinking of diatoms and partly to in situ growth. This DCM was not found to be constant either in time or space (ABBOTT et al. 1984, COON et al. 1987). In Crater Lake, Oregon, lake chlorophyll-a and primary production maximized in the 80-140 m depth, where *Tribonema* sp. occupied the 80–120 m depth zone and *Stephanodiscus* was found in the lowermost (160–200 m) stratum (LARSON et al. 1987). A possible reason responsible for DCM is behavioral aggregation of dinoflagellates. In the La Concepción reservoir, southern Spain, *Ceratium hirundinella* was found to dominate in the DCM that occurred in the metalimnion and received 1-3% of surface incident light (GÁLVEZ et al. 1988). Its duration lasted for 2–3 weeks. Mass excystment of the chrysophyte *Chrysosphaerella longispina* was found to cause a short-lasting DCM in Jacks Lake, Ontario. In the DCM observed by BIRD & KALFF (1989) in Lake Gilbert, phagotrophic chrysoflagellates (*Dinobryon sertularia, Ochromonas* sp.) were abundant and carbon uptake was based on bacteriovory at 40–79%.

Development of DCM can be especially prevalent in meromictic lakes. Their longevity, stability and position depend on water column stability and positions and the relative position of the latter to the chemoclines. Detailed case studies are available from Lake Cisó, Spain (PEDRÓS-ALIÓ et al. 1987, GASOL & PEDRÓS-ALIÓ 1991, GASOL et al. 1991), Laguna de la Cruz, Spain (MIRACLE et al. 1992) and Tasmanian lakes (CROOME & TYLER 1984).

Apart from the above cases freshwater DCM are usually related to the thermocline, especially since picoplanktonic DCM in the sea were discovered and studied in detail (e.g. CULLEN 1982). In Lake Stechlin, Germany the characteristics of the DCM were found to be very close to those in the ocean. The main growth of the picoplanktonic *Cyanobium* (formerly *Synechococcus*) occurred during the spring isothermal conditions. When the lake stratified in late May, the *Cyanobium* population formed a thin layer below the thermocline in the upper hypolimnion (15–17 m; temperature: 6–8°C) that received a variable amount of photosynthetically-active radiation at the lake surface. The measured light intensity at the depth of the DCM varied between 65 μmol m^{-2} s^{-1} on sunny and only 3.6 μmol m^{-2} s^{-1} on cloudy days at noon (GERVAIS et al. 1997, PADISÁK et al. 1997).

During the 7-year interannual phytoplankton studies on Lake Stechlin (PADISÁK et al., this volume) development, extent and erosion of DCM was monitored regularly with interesting shifts of organisms at species level. Meantime, we obtained observational data on the regular existence of cyanoprokaryotic DCM in tropical Brazilian lakes (REYNOLDS et al. 1983, BARBOSA & PADISÁK 2002). This coincidental research experience allowed us to hypothesize that high the density of cyanoprokaryotes in metalimnetic or upper hypolimnetic layers might be pre-determined by vertical structures (light, nutrients, stability of the stratification, etc.) of the water column independent of latitudinal or climatic differences. We provide case studies that suggest for any lake a DCM based on cyanoprokaryotes or other self-regulated autotrophs is likely to develop on an annual basis. This should likely happen if

1) stratification (thermocline) is stable enough for a sufficiently long period, and
2) the euphotic depth (z_{eu}) > mixing depth (z_{mix}), and moreover
3) the epilimnion is deficient in common limiting nutrients (especially P, for tropics N should also be considered). In other words, the lake's trophic state ranges from ultra-oligotrophic to mesotrophic in most cases.

Materials and methods

Description of the two study sites – temperate and tropical

Lake Stechlin is a deep oligo-mesotrophic, warm monomictic or dimictic lake in the Baltic Lake District (53°10' N, 13°02' E, 59.9 m a.s.l.; Fig. 1). The surface area is 4.25 km^2, maximum depth is 68 m and average depth is 22 m. The 12.4 km^2 catchment area is covered 80% by forests. Thermal stratification develops between April and June. The most stable thermocline is usually observed in late July. In winter, an inverted stratification may occur under the ice. Annual averages of some physical and chemical variables are given in Table 2.

The lake district of the middle Rio Doce represents one of the few natural lake systems in Brazil, formed by ca. 120 small (0.5 to 200 ha) and usually shallow (1.5 to 15 m) lakes amidst the largest remnant of the Atlantic Forest in the State of Minas Gerais, the Rio Doce State Park, Brazil (19° 48' 24"-19° 29' 24" S; 42° 38' 30"-48° 28' 18" W, 230-515 m a.s.l., 36,000 ha, Fig. 2). The area is also subjected to extensive *Eucalyptus* spp. plantations, which, together with iron and steel plants, charcoal and cellulose production, and mining activities exert considerable antropogenic impacts. Approximately one quarter of the lakes

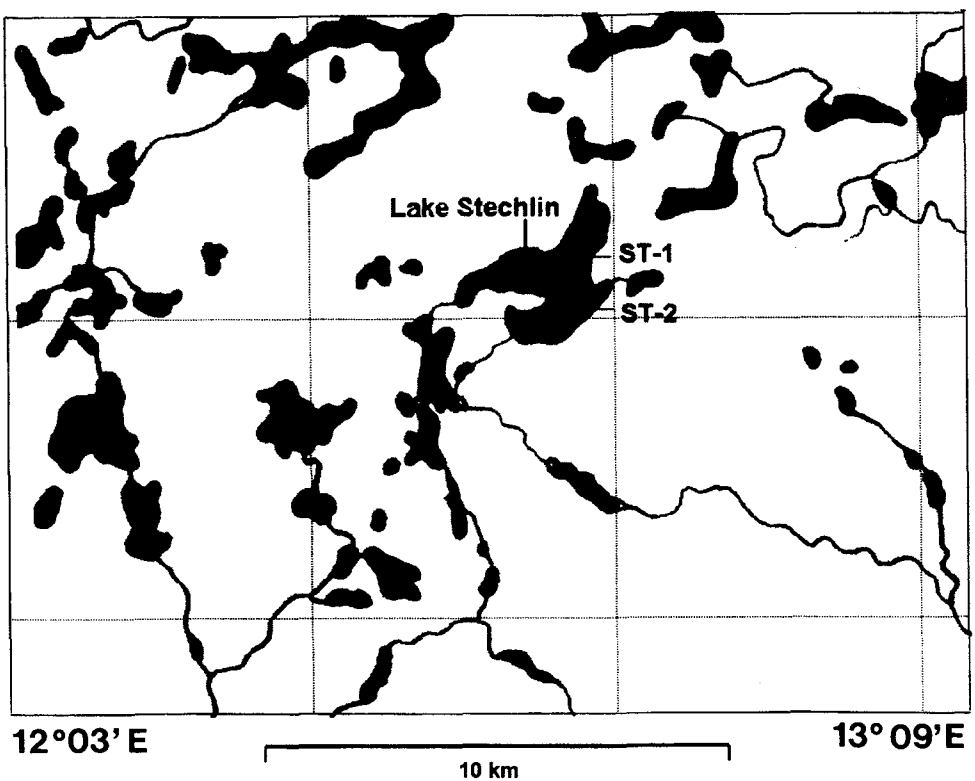

Fig. 1. Part of the Mecklenburger Lake District with Lake Stechlin (redrawn from CASPER 1985, page 17). Sampling stations are indicated as black dots.

in this area are located within the relatively unimpacted State Park. Among these lakes two have received considerable scientific attention: Lake Carioca and Lake Dom Helvécio. Lake Carioca, a mesotrophic lake (SALAS & MARTINO 1991) has a surface area of 13.2 ha and a maximum depth of 11.8 m. Lake Dom Helvécio, is oligotrophic with a surface area of 687.2 ha. With its 32.5 m maximum depth it is the deepest natural lake in Brazil. The lakes are fed primarily by precipitation but groundwater seepage also contributes significantly to their hydrological balance. Both are surrounded by secondary forests. Summer extends from October to March, a period with high precipitation and temperatures (TUNDISI 1997). Lakes Dom Helvécio and Carioca are stratified during this period while in winter they are isothermal.

Sampling, water chemistry measurements and phytoplankton analyses

In Lake Stechlin water samples were taken from 3 to 5 depths in the epilimnion weekly between middle January and end of December 1994 at a buoy situated approx. 400 m north of the Limnological Institute (water depth: 26 m; sampling station 2 on Fig. 1). These samples were mixed for analyses of phytoplankton composition, biomass and autotrophic picophytoplankton (APP) numbers.

From January 1995, samples from the 0-25 m layer (corresponding to trophogenic layer) were taken at a sampling station situated at the center of the deepest basin of the lake (Fig. 1, station 1). Sampling was carried out weekly between April and November and biweekly in the cold period (except when ice conditions interferred). APP numbers, phytoplankton composition and biomass were then established in proportionally integrated samples.

For studying vertical distribition of species, samples were taken at 0, 2.5, 5.0, 7.5, 10.0, 12.5, 15.0, 17.5, 20.0, 25.0, 30.0, 40.0, 50.0 and 60.0 m biweekly at the deepest part of the lake between May 1994 and June 1995. No such vertical sampling was carried out in 1996 and 1997. In 1998 vertical sampling for *Planktothrix rubescens* were carried out on 10th June, 23rd July and 21st August but picoplankton was counted only on 10th June. In 1999 picoplankton vertical distribution was analyzed on 10th May, 8th June, 5th July and 24th August and in year 2000 on 10th May, 5th June, 4th July and 16th August.

The analyses followed the Tecator Application Notes (ASN) 60-05/90 for PO_4-P (detection limit 0.002 mg l^{-1}; now ASN 5601), 60-03/83 for TP (detection limit 0.005 mg l^{-1}; now ASN 5602), 62-01/83 for NO_3-N, NO_2-N (detection limit 0.01 mg l^{-1}; now ASN 5621), 50-02/84 for NH_4-N (detection limit 0.01 mg l^{-1}; now ASN 5501), ASN 110-03/92 for TN (detection limit 0.01 mg l^{-1}), and ASTN 4/92 for silica (SiO_2, detection limit 0.1 mg l^{-1}). For TP measurements the unfiltered water samples were autoclaved for 30 min (134°C) after the addition of persulfate ($K_2S_2O_8$); for TN measurements the unfiltered water samples were autoclaved for 45 min (120°C) after the addition of oxisolv.

Chemical data were analyzed according to the OECD standards and standards of Deutsche Einheitsverfahren. PO_4-P, TP, NO_3-N, NO_2-N, NH_4-N, TN and silica were measured with the Perstop flow injection analysis system TECATOR FIA STAR 5010/5030. The water samples for the determination of PO_4-P, NO_3-N, NO_2-N, NH_4-N and silica were filtered through 0.6 µm membrane filters immediately after sampling. Conductivity, temperature, O_2 and pH were measured in situ (WTW LF 196, WTW OX 196, WTW, pH 196 T).

Phytoplankton species were identified using the most up-to-date phycological manuals and literature. A minimum of 400 settling units (cells, filaments or colonies) were counted in

each Lugol-fixed sample giving a counting accuracy of ± 10% for total phytoplankton. Phytoplankton biomass was estimated by geometric approximations using a computerized plankton counter (HAMILTON 1990, GOSSELAIN & HAMILTON 2000). Autotrophic picoplankton (APP) was counted, preferably immediately after sampling, in unpreserved samples. If this was not possible, unpreserved samples were deep-frozen within 1 hour after sampling and APP was counted in melted samples no later than one month after sampling.

APP cells were concentrated on a black membrane, then embedded in ~ 30% glycerine solution. Samples were analyzed with epifluorescent microscopy using a Zeiss-Axiovert 35 inverted microscope equipped with an Osram HBO 5W/AC mercury short arc lamp. Only blue excitation (Zeiss filter set 45 17 66, exciter filter 450–490 nm, FT 510, LP 520) was used for picoplankton counting because in previous trials, no significant difference was observed between counting with blue and green excitation, and green eukaryotic picoalgal cells that occasionally occur in Lake Stechlin were easier to distinguish with blue excitation. Picophytoplankton was considered here as each organism, unicellular or colonial, having cell sizes of < 2 μm. Colonial forms (*Aphanocapsa, Aphanothece, Pseudodictyosphaerium, Neocystis*) contributed only about 4% to total picoplankton numbers in this study. They were included in the picoplankton because they often lose cells and these lost unicells functionally belong to this group. See more details in PADISÁK et al. (1997).

Two diurnal cycles were investigated in the two tropical lakes, respectively (on 11/12 February 1999 and on 17/18 February 2000 in Lake Carioca and on 15/16 January 1999 and 15/16 February 2000 in Lake Dom Helvécio). Environmental data (temperature, conductivity, pH, dissolved oxygen and redox potential) were recorded every 3 hours with a Horiba profile sensor at 0.5 m increments. Water chemistry data (major nutrients) were measured at depths corresponding to 100%, 10% and 1% of the surface irradiance (measured by a Li-Cor quanta sensor) and in the aphotic zone at the same time intervals according to methods described in APHA (1992).

Phytoplankton samples were taken at a fixed sampling station using a van Dorn sampler at the same time intervals from water depths 0, 1, 3, 5, 6, 7 and 9 m in lake Carioca and 0, 1.5, 3, 4.5, 6, 7.5, 9, 12 and 20 m in lake Dom Helvécio. These samples were analyzed as described for Lake Stechlin but APP was not counted (according to microscopic observations, algal cells < 2 μm were very rare).

Relative water column stability (RWCS) was calculated by comparing the density gradient of the whole water column to the density difference between 4°C and 5°C pure water (density data from PERRY 1950) using the following formula:

$$RWCS = \frac{D_h - D_s}{D_4 - D_5}$$

Where D_h is the density of the bottom waters, D_s is the density of the surface water, and D_4 and D_5 are the densities of water at 4°C and 5°C, respectively (WELCH 1992). For lake Stechlin the depth of 20 m was considered as "bottom water" because data from deeper strata were not always measured. In this lake, temperature differences between bottom water and the 20 m layer are usually less than 1°C. For the tropical lakes subsurface and above-bottom temperatures were used.

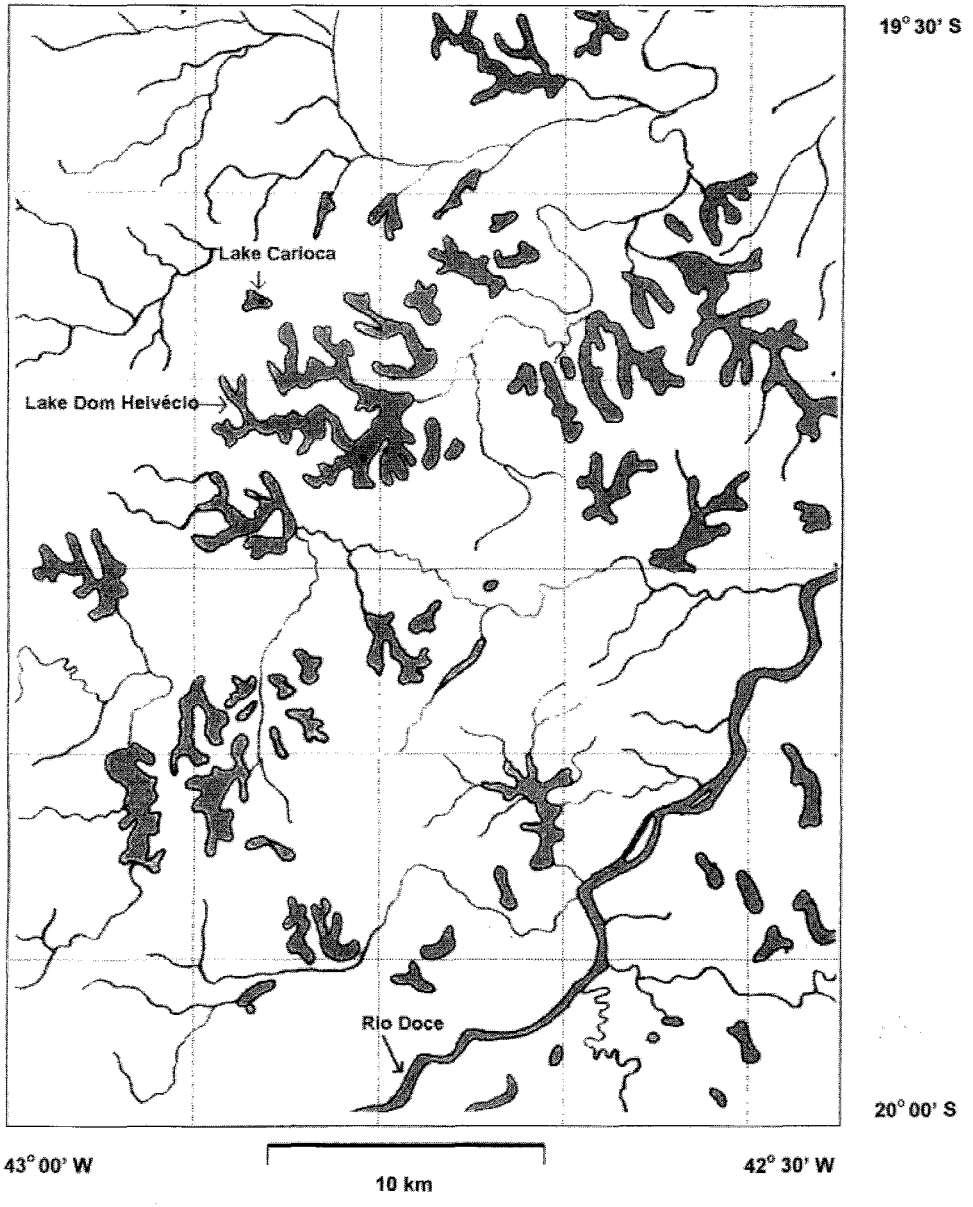

Fig. 2. Part of the Rio Doce Valley Lake District with Lake Carioca and Lake Dom Helvécio (redrawn from TUNDISI & SAIJO 1997, appendix: Map and Photos). Sampling stations are indicated as black dots.

Results and discussion

Species composition

Between 1994 and 2000 two cyanoprokaryota species contributed to the DCM in temperate Lake Stechlin, Germany. The "*Synechococcus*-like" *Cyanobium* sp. (description in PADISÁK et al. 1997; cf. KOMÁREK 1996) formed a DCM every year except in 1998 when *Planktothrix rubescens* (DC. ex GOM.) ANAGN. et KOM. was the major contributor. During the May–June period sinking diatoms may temporarily contribute to the DCM (PADISÁK et al., this volume).

In tropical Lake Dom Helvécio, the main contributor of the DCM was *Cylindrospermopsis raciborskii* (WOLOSZYNSKA) SEENAYA & SUBBA-RAJU. This species has a tropical origin despite being recently wide-spread in the temperate region, and it is known as a species that can form very dense suspended, sometimes toxic, blooms. However, original locations were tropical lakes of rather low trophic status that allowed for the supposition that the shade tolerance of this species might have evolved in a tropical DCM (PADISÁK 1997). Lake Dom Helvécio is the first tropical lake where this species was found in the DCM (BARBOSA & PADISÁK 2002).

The major contributor of DCM in tropical Lake Carioca, Brazil, in 1998 was a species that has probably not been described yet. REYNOLDS et al. (1983) found an unispecific metalimnetic maximum of "*Lyngbya limnetica* LEMMERMANN" in Lake Carioca in February-March 1981 and provided a correct morphological description of the species involved. Accordingly, and in agreement with our investigations, the cell width was 1.9–2.7 μm, and the length was 5–8 μm, with slight narrowing at adjacent cells. Filaments were embedded in fairly well visible mucilage that was frequently, but not necessarily, substantially longer than the filament itself. The most characteristic feature of the species is the high number of irregularly arranged, high-contrast intracellular structures. These made the appearance of the filaments similar to that of *Limnothrix redekei* (VAN GOOR) MEFFERT, although the contrasting particles or vacuoles were larger because, of larger cell sizes. The presence of the mucilage excludes the species from *Limnothrix*. On the other hand, the presence of contrasting intracellular structures excludes its identification as *Planktolyngbya limnetica* (LEMMERMANN) KOM.-ANAGN. (valid synonym for *Lyngbya limnetica*). The DCM that we found in Lake Carioca in 1998, however, was not monospecific: other species like *Limnothrix planktonica* (WOLOSZ.) MEFFERT, *Romeria* sp., *Synechocystis* sp., *Pseudanabaena* sp. and *Planktothrix* sp. also contributed to the DCM.

Seasonal development and regularity

The DCM species are important contributors to the phytoplankton in Lake Stechlin. The *Cyanobium* population (Fig. 3) develops regularly during the spring isothermal period and forms a DCM when the lake stratifies (details in PADISÁK et al. 1997). Layering is usually followed by active growth which makes the seasonal pattern bimodal (maxima in May – early June, and then again, in August) like in 1994, 1996 and 1997. In other years the seasonal pattern is monomodal with a single spring maximum (1995) or single July maximum (1998, 1999 and 2000). Nevertheless, growth of *Cyanobium* is highly regular and seasonal independently from slightly different seasonal patterns. *Planktothrix rubescens* occurred only sporadically in 1994–1997, however, it was typically found in samples from the isothermal period. Its growth started after the thermocline deepened in 1997 and continued throughout the water column until the onset of thermal stratification. When the thermocline developed in

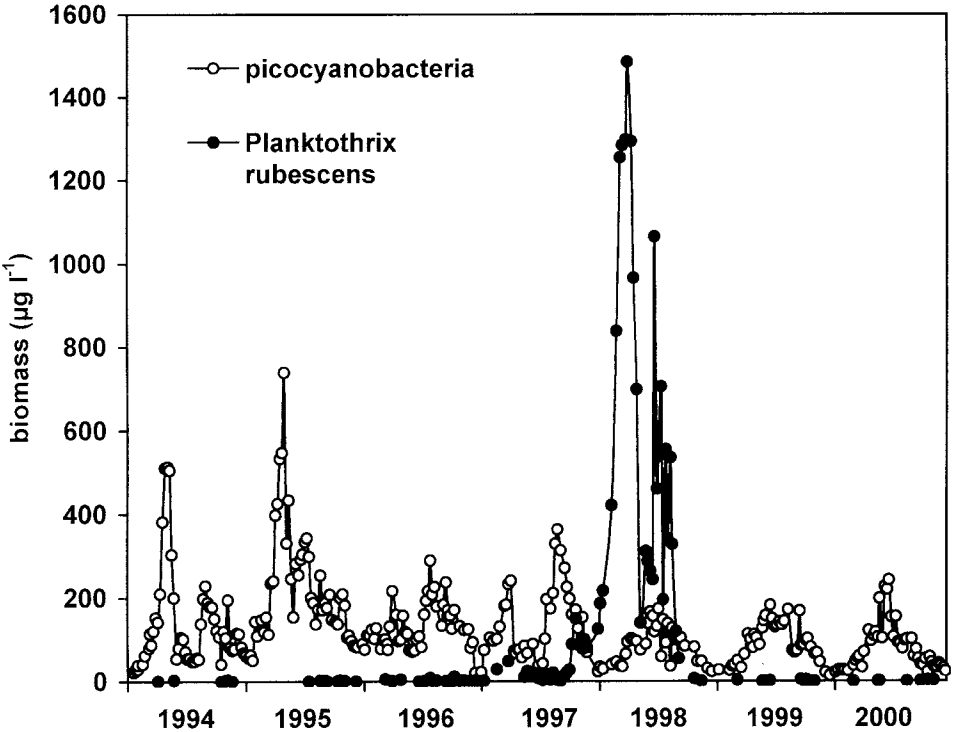

Fig. 3. Biomass (µg l^{-1}) of picocyanoprokaryotes (dominant species: *Cyanobium*) and *Planktothrix rubescens* in Lake Stechlin between 1994 and 2000. Data represent average of the upper 25 m which includes DCM.

1998, part of the population remained sinking into the hypolimnion (chapter about vertical patterns) and another portion formed a dense DCM within which it continued its population increase (therefore the presence of a second peak in 1998). After the thermocline breakdown in 1998, *P. rubescens* occurred in the samples only sporadically until the end of 2000. Reasons for *P. rubescens* outbreak have not been clarified presently. There were no marked differences in the water chemistry prior to its mass appearance. The only unusual event was the extremely long-lasting ice-cover period in the winter of 1995/1996 (SCHEFFLER & PADISÁK 2000), after which *P. rubescens* occurred more and more regularly in the samples and reached higher and higher biomass. Note that growth of the *P. rubescens* population did not follow the "classical pattern" (c. f. SOMMER et al. 1996) of phytoplankton succession because it overlapped at least two vegetation periods.

There has been no regular monitoring program carried out on the tropical Rio Doce Valley lakes in Brazil; research is mostly restricted for intensive sampling programs over short periods of time. Therefore, it is unknown how regular the DCM development would be in lakes Carioca and Dom Helvécio; the repetitive nature of the species composition of the DCM is also unknown. Nevertheless, sporadic information (partly as vertical distributions of chlorophyll *a* throughout the water column) allows us to suppose that the development of DCM occurs each year (REYNOLDS et al. 1983, REYNOLDS 1997a, MATSUMURA-TUNDISI et al. 1997).

Despite the lack of a regular monitoring program in these lakes there are several sporadic and concentrated data to support the suggested regularity of the DCM during stratification periods. The occurrence of deep chlorophyll-a maxima for lake Carioca was demonstrated first by BARBOSA & TUNDISI (1980) when a maximum of 72.4 μg l^{-1} chlorophyll a was recorded at 9 m in January 1978 of which 63% was measured as pheophytin. At the time attention was given to the probable accumulation of phytoplankton material at this layer. This DCM was later described as formed mainly by *Lyngbya limnetica* (REYNOLDS et al. 1983). PONTES (1980) reported chlorophyll a maxima (5.0–10.0 μg l^{-1}) in Lake Dom Helvécio at 20 m depth in January, March and May 1978, although chlorophyll a maxima (c. 10 μg l^{-1}) were also recorded within the upper layers (3 m) in July 1977. Furthermore, from studying seasonal fluctuations of Cladocera populations in 5 lakes of the Rio Doce Lake District, SANTOS (1980) reported chlorophyll a maxima and high concentrations during the stratification period. For Lake Dom Helvécio, the highest concentrations (c. 6.5–8.5 μg l^{-1}) were recorded between January and March 1978 which are approximately 3 times higher than the ones recorded in the surface layers. In Lake Carioca, the highest concentrations were also recorded in the bottom layers during the stratified period (September–April) with chlorophyll a values as high as ca. 335 μg l^{-1} in March 1978. Finally, in a comparative study of the same 5 lakes (ALEIXO 1981) demonstrated the occurrence of DCM during the stratified period through bi-monthly samplings at depths corresponding to 100%, 50%, 25%, 10% and 1% of surface irradiance, and at the aphotic layer. The highest concentration (ca. 5 μg l^{-1}) in Lake Dom Helvécio was recorded at 20 m depth in March 1978. In Lake Carioca at this time, 35 μg l^{-1} was recorded at 7 m and a much higher value (ca. 365 μg l^{-1}) was recorded at the bottom of the lake (9 m).

Vertical distribution of phytoplankton biomass

As described in PADISÁK et al. (1997), in Lake Stechlin standing crop of picoplankton DCM develops annually during isothermal period. Then, a subsequent layering during the thermocline development leads to DCM development where subsequent growth occurs during the stratified period. The maximum extent of picoplanktonic DCM occurred at various times between May and August in Lake Stechlin. In 1994 the highest density occurred in May (Fig. 4A), in 1995 the maximum was observed it was during June (Fig. 4B) while in 1999 (Fig. 4C) and 2000 (Fig. 4D) in July. In each case the highest biomass was recorded at 15 m below the lake surface. This was the same for the year 1998 (Fig. 5B) when maximum biomass also occurred at 15 m. Below 25–30 m individuals of this population were rare and rather evenly distributed. During the period 1994–2000 a significant population of *Planktothrix rubescens* developed, but only in 1997-1998. In June 1998 this population was poorly represented in the epilimnion of the lake (Fig. 5A, B) but formed a sharp upper hypolimnetic maximum in the 20–30 m water layer. Data from June-August (Fig. 5A) clearly showed that quite a significant accumulation of sinking filaments occurred in the deep (60–65 m) hypolimnion (Fig. 5A). Such a phenomenon was not observed for the *Cyanobium* population. In 1998, when *Planktothrix* was the main contributor of the DCM, biomass in the upper hypolimnion exceeded that of other years by approximately 10-fold, and *Cyanobium* reached a density of about half of its maximum density in other years. The vertical distribution of the two populations shows a spatial segregation: *Cyanobium* accumulated at 15 m like in other years while *Planktothrix* exhibited maximum density at 20–30 m (Fig. 5B).

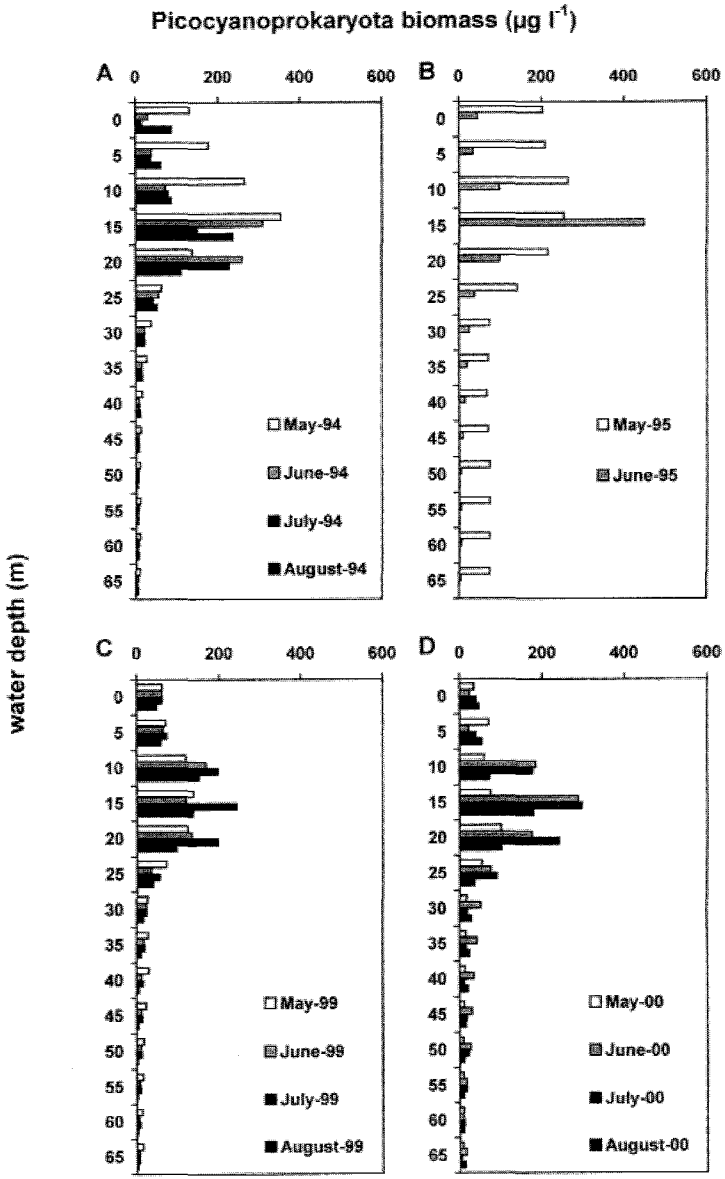

Fig. 4. Vertical distribution of picocyanoprokaryotes (biomass, µg l^{-1}) on some sampling dates in years 1994 (A), 1995 (B), 1999 (C) and 2000 (D) in Lake Stechlin.

On 11 January 1999 a sharp DCM was found in tropical Lake Carioca, exhibiting a peak at 6-7 m depth (Fig. 6). Species other than Cyanoprokaryota occurred characteristically in the upper water layers. In Lake Dom Helvécio, the DCM-forming species was *Cylindros-*

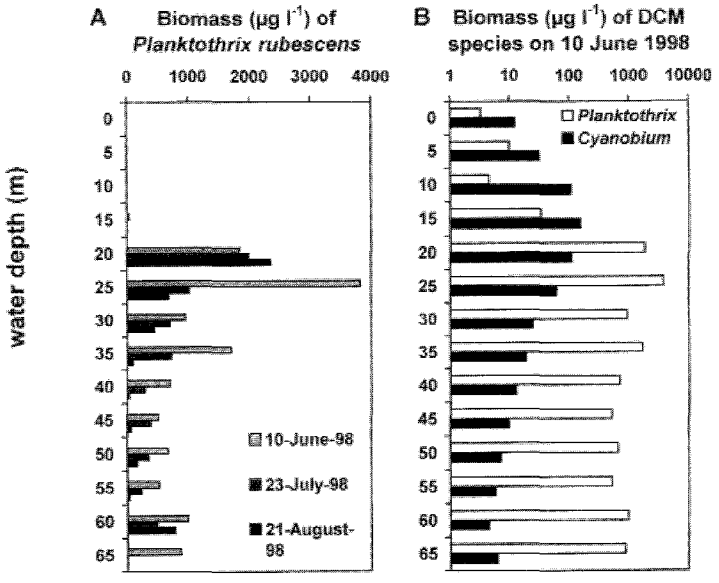

Fig 5A. Vertical distribution of *Plankothrix rubescens* (biomass µg l^{-1}) on 10 June, 23 July and 21 August in Lake Stechlin and **(B)** Vertical distribution of *Cyanobium* and *Planktothrix* biomass (µg l^{-1}) on 10 June 1998 in Lake Stechlin. Note the logarithmic scale for biomass.

permopsis raciborskii (Fig. 6). Planktonic desmids dominated in the epilimnion of the lake and *C. cuspis* also occurred but, it did not peak in the metalimnion (Barbosa & Padisák 2002).

Vertical gradients

The temperate Lake Stechlin is a warm monomictic (in years with severe winters it is dimictic) lake. Relative stability of the water column stratification increases usually in May (Fig. 7A) and reaches a maximum of 220 to 350 RWCS during the summer when maximum temperature differences between surface and hypolimnetic waters spans about 16–18°C. The dataset between 1994 and 2000 shows that there might be substantial differences between stability of summer stratification in different years. The tropical Lake Carioca and Lake Dom Helvécio are also warm monomictic lakes which are stratified in the wet season (November–April) and isothermal in the dry season (May–October). In the stratified period water column stability also maximizes close to 300 (Figs. 7B and 7C). Because of the lack of systematic sampling, data shown in Figs. 7B and 7C were assembled from our own measurements and different publications (Tundisi & Saijo 1997). Although the data base is very poor, variation between and within dry season and wet season data was obvious. This variation is mostly due to short-term events, namely substantial surface temperature differences even at a scale of single days. Measurements from 15/16 and 17/18 (Fig. 7D) show that the daily variance of relative stability may range between 230 and 340 as a consequence of inten-

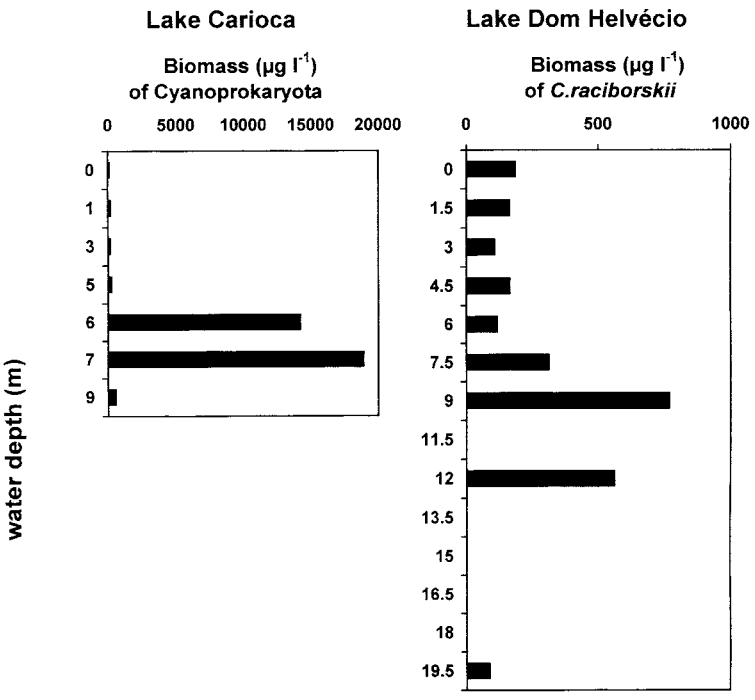

Fig 6. Biomass (µg l^{-1}) of cyanoprokaryota in Lake Carioca on 11 January 1999 (left panel) and biomass (µg l^{-1}) of *Cylindrospermopsis raciborskii* in Lake Dom Helvécio on 15 January 1999 (right panel).

sive daytime warming and nocturnal cooling (partial atelomixis; more data in BARBOSA & PADISÁK 2002). Nevertheless, despite the only about ca. 8 °C degree temperature difference between surface and bottom waters for these two tropical lakes (Fig. 8A), relative stability of their water columns, in terms of water density, are comparable (or even higher) than in temperate lakes (WETZEL 2001, PERRY 1950) as demonstrated in Fig. 8B. The pycnocline in the three lakes can be found at 5 m in Lake Stechlin, 4.5 m in Lake Carioca and 8 m in Lake Dom Helvécio.

Euphotic depth (defined as water depths where 1% of surface irradiation occurs; Fig. 8C) in the three lakes were: Lake Carioca – 7.5 m; Lake Dom Helvécio – 11 m and Lake Stechlin – 17.5 m. As the data show, euphotic depth exceeds mixing depth (calculated from the position of the pycnocline) in each of the three lakes; z_{eu}/z_{mix} ratios for the three lakes were: Lake Carioca – 1.67; Lake Dom Helvécio – 1.38 and Lake Stechlin – 3.50.

Lake Stechlin is an oligo-mesotrophic lake where dissolved P has been characteristically less than the value of 10 µg l^{-1} for the entire year above which P availability does not limit phytoplankton growth (SAS 1989). Higher values may occur for short periods after the autumnal overturn (data in PADISÁK et al. 1998). Dissolved NO_x forms exhibit a characteristic seasonal distribution in their vertical pattern: during the isothermal period values of about 40–70 µg l^{-1} NO_x-N were measured throughout the water column, while epilimnetic values

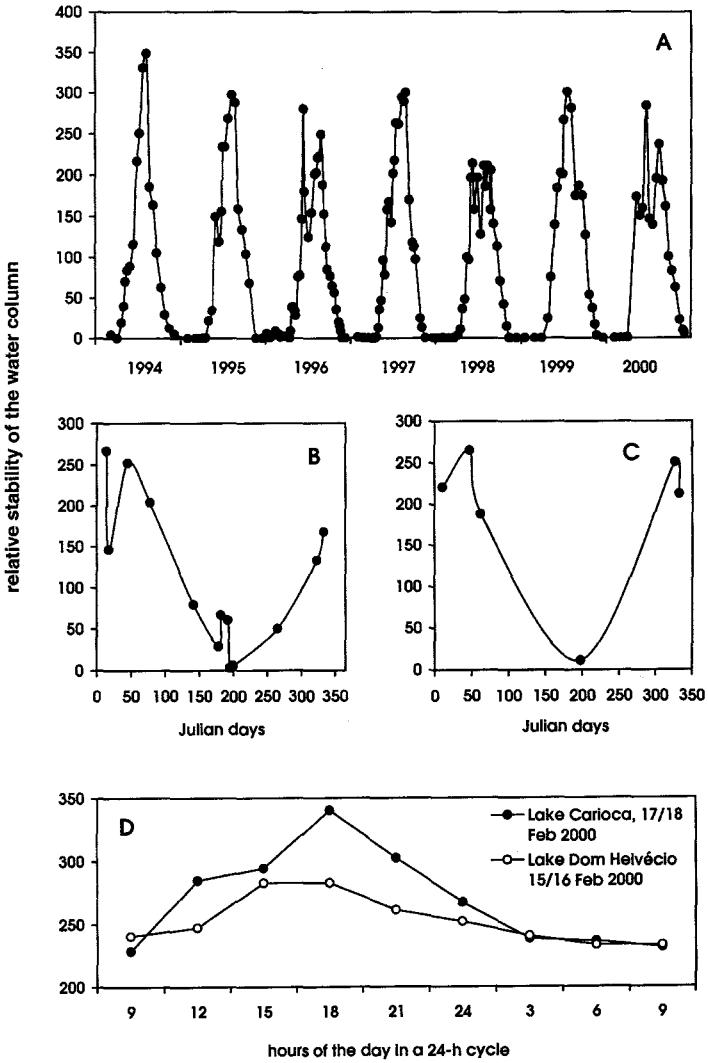

Fig. 7. Relative stability of stratification
(A) in Lake Stechlin between 1994 and 2000 in Lake Stechlin;
(B) in Lake Dom Helvécio and
(C) Lake Carioca during an idealized annual cycle (days are given in Julian days; data are from different years: from our own measurements and from TUNDISI & SAIJO 1997);
(D) During a daily cycle in Lake Carioca (17/18 February 2000) and Lake Dom Helvécio (15/16 February 2000).

dropped to close to zero during the stratified period and values within the hypolimnion increased to 100–150 μg l^{-1} NO_x-N. Concentrations of NH_4^+-N were low: from ~ 0–30 μg l^{-1} (in the isothermal period) to 40–70 μg l^{-1} (in both the epi- and hypolimnion during the strati-

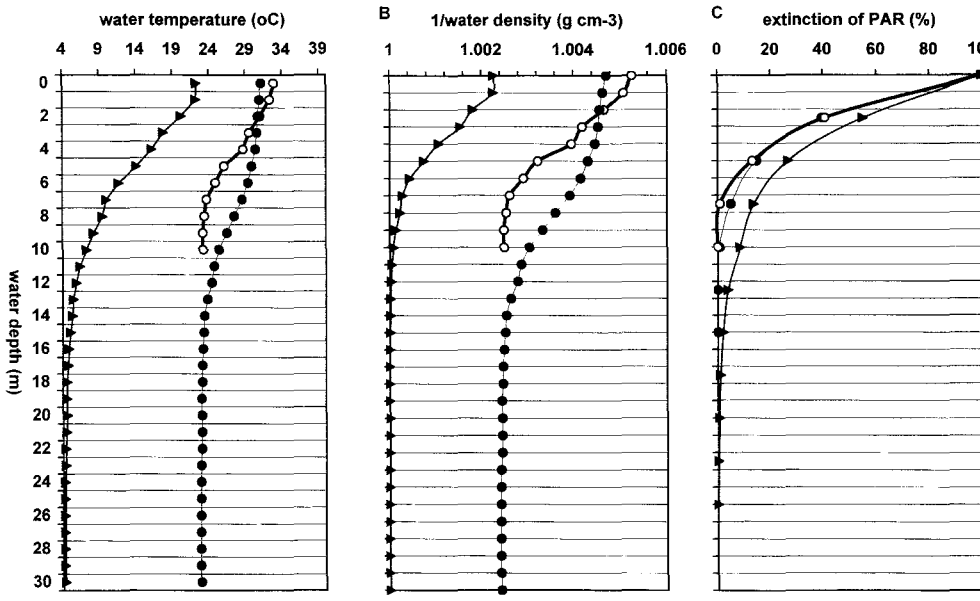

Fig. 8. Vertical distributions of (A) water temperature (°C), (B) reciprocal of water density (g cm^{-3}) and (C) light attenuation (as percent of subsurface irradiation measured originally as µE m^{-2} s^{-1}) in Lake Carioca (¢), Lake Dom Helvécio (●) and Lake Stechlin (▲) during the stratified periods of the lakes in 2000.

fied period; data in PADISÁK et al. 1998). Therefore, phytoplankton growth can also be limited also by N availability during the stratified period.

In Lakes Carioca and lake Dom Helvécio there are no coherent data about seasonal variations in inorganic nutrient availability, however, bioassay experiments reported P-limitation and slightly excessive amounts of nitrogenous compounds (NAKAMOTO & HINO 1987). According to data given in Tables 2 and 3, PO_4-P remained below the limiting value (10 µg l^{-1} according to SAS 1989) except a single epilimnetic value in Lake Carioca in 1999. NO_x-N concentrations were rather low in the two tropical lakes with slightly higher values in the hypolimnion. In Lake Stechlin NO_x-N exhibited considerably higher values in the hypolimnion than in the epilimnion, moreover, differences between the two strata were more obviousd during the stratified period (PADISÁK et al. 1998). The different patterns between the tropical and the temperate lakes can be explained by nitrate consumption during denitrification and/or nitrate-respiration in the sub-oxic/anoxic hypolimnia of the tropical ones. Concerning NH_4^+-N, there were minor concentration differences in Lake Stechlin between epi- and hypolimnetic data. In both tropical lakes epilimnia are relatively poor in NH_4^+-N and, in contrast, hypolimnetic records are rather high. During the stratified period, communities below the pycnocline are not limited by scarcity of inorganic N-compounds because NO_x-N (especially nitrate) is above the limiting concentration in Lake Stechlin and NH_4^+-N is above the limiting concentration in Lake Carioca and Lake Dom Helvécio. Soluble reactive silica concentrations are above the limiting level in all of the three lakes in all seasons.

General aspects and conclusions

Occurrence of deep chlorophyll maxima (DCM) in stratified lakes can be temporal event (sinking diatoms, active habitat selection of motile flagellates, mass-encystment of chrysophytes, etc. as listed in the introduction) or a more pronounced event, like the development of more or less dense layer of cyanoprokaryotes. Since DCM (primarily dominated by "*Synechococcus*-like" coccal picocyanobacteria) were discovered much earlier in the world ocean than in stratified lakes, hypotheses about reasons leading to their development in marine environments are numerous. Historical data in early freshwater plankton literature can also be found but without functional recognition of vertical distribution patterns. ANDERSON (1969) suggested that DCM originated from photosynthetically active phytoplankton populations adapted to low light. HERBLAND (1983) related the DCM to vertical distribution of nutrients. TAKAHASHI & HORI (1984) related the DCM to a decrease in sinking rates of nutrient impoverished cells, while TAGOUCHI et al. (1988) hypothetized that the DCM was rather due to increased cellular chlorophyll content than to a real increase in phytoplankton biomass. Other studies related the DCM to coupled physical/biological processes. BANSE (1987) related the DCM and the associated nutricline (especially nitracline) to atmospheric conditions and the mixed layer depth. KIEFER & KREMER (1981) showed that the DCM is mainly determined by the seasonal dynamics of the thermocline and many other physical features (tidal mixing, internal waves, instabilities of shelf/slope front, etc.), some of which are practically exclusive for oceanic conditions. RAMIRO et al. (1992) concluded that the DCM is primarily the result of a balance between upward nutrient flux and light characteristics.

Apart from REYNOLDS' (1992b) seminal paper on the development of vertical structures and corresponding biological response of phytoplankton species, there are few studies about freshwater DCM and reasons for their development. Most of the studies concentrated on buoyancy regulation and photosynthetic activity of the best known freshwater DCM species, *Planktothrix rubescens* (WALSBY 1994, 1998, MICHELETTI et al. 1997, WALSBY et al. 1998). In his review paper about the Rio Doce valley lakes, REYNOLDS (1997a) listed the theoretical prerequisites for development of DCM as: sufficiently stable stratification, chemical gradients of the major nutrients, photic as well as redox gradients. He concluded that strong gradients in assimilable nitrogen (especially ammonia) is the most likely factor that provides selective ecological advantage for DCM species in these lakes and noted that the ability of chromatic adaptation was also an essential factor. GERVAIS et al. (1997) attributed occurrence of DCM to low phosphorous concentration and light quality (dominance of wavelengths between 500 and 600 nm which corresponds to absorbance of phycoerythrin) in Lake Stechlin.

Temperature gradients in the tropical lakes are weaker than in temperate ones therefore their metalimnia form relatively wide layers. This study demonstrated that in terms of water density the gradient is similarly sharp in tropical and temperate lakes, therefore their resistance to vertical mixing is comparable during the stratified periods. In Lake Stechlin wind-driven mixing is the main factor in determing the position of the thermocline. In extremely well wind-sheltered Lake Carioca the vertical mixing is driven by convective currents, generated by nocturnal cooling and daytime heat accumulation, leading to complete atelomixis in the isothermal dry season and to partial atelomixis in the stratified period during the wet season (BARBOSA & PADISÁK 2002). In Lake Dom Helvécio, both wind and daily temperature differences contribute to the location of the pycnocline depth and, as a matter of fact, in the three investigated lakes this one had the deepest pycnocline. Nevertheless, all three lakes

have a quite stable stratification below which a fairly high level of environmental stability may occur.

Light levels at the depth of the DCM fluctuated around 1% of subsurface light and corresponded to 5–25 μmol m^{-2} s^{-1} depending on actual weather conditions. In this range photosynthesis of shade tolerant algae, like *Synechococcus*-like cells, *Planktothrix, Limnothrix, Cylindrospermopsis*, is not or at least not severely limited by light (summary in PADISÁK, in press). Since these species are usually sensitive to light intensities above the saturation level, it can be supposed that in the epilimnetic layer of the tropical lakes (which, due to daily mixing, is also a layer with high environmental constancy) inhibitory light intensities may occur.

In Lake Stechlin, the presence of nutriclines during the stratified period was evident. PO_4-P concentrations are somewhat higher in the hypolimnion, P-turnover times are rather short (7–24 min) and at the depth of the DCM the bulk of PO_4-P is utilized by the fraction < 1–3 μm. Differences in epilimnetic and hypolimnetic NO_x-N (practically NO_3-N) during the stratified period may exceed 100-fold, which, combined with the overall scarcity of NH_4-N separates the water column into two distinct layes: a N-deficient epilimnion and an N-sufficient hypolimnion. Therefore, just like in the oceans, the presence and position of the dominant picocyaprokaryote DCM can be clearly related to the nitracline.

Chemical gradients of essential nutrients are a logical pre-requirement (REYNOLDS 1997a) for the DCM since the algae must have some advantage for living in the dark (in temperate lakes it is also cold). From substantial differences in NH_4-N concentrations REYNOLDS (1997a) pointed out that the hypolimnetic availability of assimilable nitrogen could lead to the development of the DCM in these lakes. In our study 38 to 55-fold (Lake Dom Helvécio) and 17 to 31-fold (Lake Carioca) differences were found between epi- and hypolimnetic records of total inorganic N forms. However, epilimnetic concentrations (41–52 μg l^{-1} N_{inorg} in Lake Dom Helvécio; 28–30 μg l^{-1} N_{inorg} in Lake Carioca) corresponded to 1/3–1/2 of the level above which N availability certainly was not limiting (100 μg l^{-1}, SAS 1989). Hypolimnetic concentrations well exceeded the limiting levels. Based on published measurements (TUNDISI et al. 1987, REYNOLDS 1992a, 1997a) it was concluded that the range of 5–20 mg l^{-1} [probably a misprinting in REYNOLDS (1997a) as the dimension of the data is not mg l^{-1} but μg l^{-1}] for PO_4-P cannot limit phytoplankton growth. These studies did not support this finding. With no exception, severely limiting PO_4-P-concentrations were found in the epilimnia (0.3–0.9 μg l^{-1}; actually these data are below the detection level of the molybdate method, therefore they are considered as non-detectable concentrations); hypolimnetic data ranged between 2 to 4.2 μg l^{-1} with a single high measurement of 14.8 μg l^{-1} in Lake Carioca. Therefore, in Lakes Carioca and Dom Helvécio, phosphorus more than nitrogen in 1999 and 2000 can be considered as major nutricline factor.

Most of the studies from freshwaters report about monospecific DCM cyanoprokaryotes. This is not surprising since the relatively narrow layer that may support the DCM possesses a high environmental stability, therefore it would provide appropriate circumstances/time for selection of the best adapted species. However, a monospecific feature is in no way obligatoty. In Lake Carioca, the DCM was composed by a mixed filamentous assemblage in both years with dominance of the so-called "*Lyngbya*" sp., which in the early 1980s appeared as almost monospecific maximum. The mono- or multispecific features of the DCM in Lake Carioca cannot be explained because regular data and knowledge about developmental pattern of the DCM are missing. However, weather-driven daily changes in the extent of atelomixis may be superimposed on an intermediate frequency of disturbance (PADISÁK et al.

Table 2. Annual averages of some physical and chemical variables in Lake Stechlin between 1994 and 2000 from routine measurements at the deepest basin of the lake (TP: total phosphorus; TN: total nitrogen; pH and conductivity data refer to the whole water column [0–67 m]; * annual average 0–25 m; ** annual average 25–67m).

	1994	1995	1996	1997	1998	1999	2000 (Jan-August)
Secchi transparency (m)	8.2	7.9	8.4	9.3	9.4	9.6	9.0
Oxygen saturation (%)	111*; 87**	104*; 83**	100*; 69**	103*;7888	97*; 75**	103*, 83**	106*, 86**
pH	8.28	8.17	8.07	7.99	8.16	8.09	8.20
Conductivity (µS cm-1)	280	270	283	286	285	281	303
PO4-P (µg l^{-1})	2.5*; 8.0**	1.9*; 6.0**	2.0*; 10.0**	2.1*; 15.3**	2.0*; 11.8**	2.2*; 7.7**	2.0*; 8.0**
TP (µg l^{-1})	16.3*; 19.0**	16.0*; 19.0**	16.0*; 25.0**	10.0*; 24.0**	10.4*; 21.5**	10.8*; 15.3**	10.0*; 16.0**
NOx-N (µg l^{-1})	18*; 94**	21*; 72**	11*; 92**	19*; 48**	17.*; 72**	33*; 89**	28*; 73**
NH_4-N (µg l^{-1})	32.5*; 78**	25.3*; 25.0**	23.1*; 30.0**	16.2*; 20.0**	18.0*; 31.0**	49.8*; 30.0**	19.0*; 28.0**
TN(µg l^{-1})	587*; 499**	444*; 442**	489*; 508**	445*; 620**	552*; 485	433*; 339**	387*; 448**
SRSi (µg l^{-1})	620*; 1610**	640*; 1330	675*; 1695**	751*; 1690	990*; 1530**	976*; 1461**	450*; 1200**

Table 3. Some limnological features of Lakes Carioca and Dom Helvécio at two selected depths of the water column corresponding, respectively, to a depth within the epilimnion and the hypolimnion, during the stratified periods of 1999 and 2000.

	Lake Carioca Jan. 1999		Feb. 2000		Lake. Dom Helvécio Jan. 1999		Feb. 2000	
Depth (m)	1.0-1.55	9.0	1.5	9.0	1.5	20.0	1.5	18-20
pH	6.4	6.1	6.1-6.8	5.6–5.9	7.4	6.3	6.8–7.7	5.7–6.4
Conduct.($\mu S\ cm^{-1}$)	20	99	28	105–183	29	52	36	61–73
Diss. Ox. ($mg\ l^{-1}$)	5.3–7.0	0.0	7.6–8.4	0.4–0.6	7.0–7.8	0.0	8.4–8.8	0.4–0.6
Alk.($meq.CO_2\ l^{-1}$)	-	-	0.3	0.6–0.8	-	-	0.3–0.4	0.4–0.5
Chl-1.-a ($\mu g\ l^{-1}$)	-	-	6.9–15.5	41.1–90.9	-	-	2.7–21.9	10.2–40.1
PO_4-P ($\mu g\ l^{-1}$)	-	-	0.4–14.8	0.3–2.9	-	-	0.7–4.2	0.9–2.0
$P_{total-1}$ ($\mu g\ l^{-1}$)	-	-	13.9–20.3	33.1–52.3	-	-	6.5–16.4	7.7–15.4
NH_4^+ ($\mu g\ l^{-1}$)	6.3–42.1	1025.3–1640.2	8.4–62.7	716.6–1966.5	6.6–31.3	637.2–875.3	1.9–41.2	6.6–743.1
NO_2^- ($\mu g\ l^{-1}$)	0.8–4.3	2.4–15.8	0.5–6.2	1.3–10.7	7.4–12.3	5.3–17.0	0.1–2.3	0.6–6.3
NO_3^- ($\mu g\ l^{-1}$)	10.4–18.2	13.3–28.7	8.2–18.3	14.7–35.1	0.8–1.6	1.2–6.3	1.1–13.2	3.7–38.3
SiO_2 ($mg\ l^{-1}$)	3.1–4.3	3.3–4.1	2.1–2.5	1.9–3.1	4.4–5.4	3.8–4.7	2.6–3.2	2.8–3.8

1993) on the layer beyond the pycnocline, and this may explain the failure of complete competitive exclusion.

In Lake Stechlin an interesting alteration of DCM-dominant species occurred: *Cyanobium* formed the DCM in each year except 1998 when a high amount of *Planktothrix* was superimposed on the regular *Cyanobium* DCM, and the two species coexisted. According to TILMAN's (1982) models and experiments about species co-existence or to HARDIN's (1960) competitive exclusion theory (only as many species may co-exist as the number of limiting factors) we have to suppose that growth of *Cyanobium* and *Planktothrix* were limited by different factors. Morphological and therefore morphoecological features of the two species are quite different. *Planktothrix* is a filamentous organism, and therefore acts as a good "antenna" to collect light (REYNOLDS 1997b) while *Cyanobium* with its wide ellipsoid shape is not. Since one "average" *Planktothrix* filament could comprise approx. 55,000 *Cyanobium* cells, we may deduce that *Planktothrix* must have a much smaller light extinction coefficient per unit biomass than *Cyanobium*. The position of *Cyanobium* and *Planktothrix* populations in June indicated spatial segregation: *Cyanobium* (like in other years) had a maximum density at 15 m while the *Planktothrix* maximum was at 20 m indicating that *Planktothrix* is a superior competitor for light. The *Planktothrix* population started to develop in August 1997, with its population density almost continuously increasing during the isothermal period. Since the availability of PO_4-P, the ultimate limiting factor of primary production in Lake Stechlin, increased annually only after the autumnal overturn (PADISÁK et al. 1997, 1998), the growing *Planktothrix* population had the opportunity to take up and store as much phosphorus as its threshold level allowed since *Cyanobium* usually started to increase only in January. The fact that *Cyanobium* managed to reach a similar density than in other years allows us to conclude that this species has a higher P-affinity and its threshold for P uptake is smaller than that of *Planktothrix*. Indeed, morphological features of *Cyanobium* allow us to raise this conclusion because large surface area per unit biomass enhances nutrient uptake and small cell size minimizes transport distances within the cells; both factors enhance the utilization of nutrients. In this case, the surface/volume (S/V) ratio of Planktothrix is 0.57 and S/V of *Cyanobium* is 6.73. By this calculation the 55,000 *Cyanobium* cells that one *Planktothrix* filament could accommodate have 12-times larger surface than the *Planktothrix*. Based on this argument it is reasonable to suppose that coexistence of the two species in the upper hypolimnion of Lake Stechlin in 1998 was stable because *Planktothrix* was limited by P and *Cyanobium* was limited by light. This might explain the presence of morphoecologically very different species in the same habitat, and would moreover allow us to predict that in severely P-limited deep lakes the availability of P (or even N) will be a stronger selective factor than light. Therefore picocyanobacteria will form the DCM and in lakes where P (nutrients) are more scarce and filamentous forms will have selective advantage in more light limited environments.

Studies on photoadaptation strategies of phytoplankton species to low light intensities (REYNOLDS 1997b) are accumulating. There are two typical and common kinds of low-light environments: shallow, eutrophic or even hypertrophic lakes with frequent mixing and the upper hypolimnia of deep lakes with moderate (maximum mesotrophic) trophic status. Occurrence of *Planktothrix rubescens* is well known in the upper hypolimnia of temperate lakes while the closely related *P. agardhii* occurs commonly in shallow, polimictic, eutrophic waters. Differentiation between the two species is frequently problematic since *P. agardhii* may also have a pink color when occurring in deep layers (UTKILEN et al. 1985). *Cylindros-*

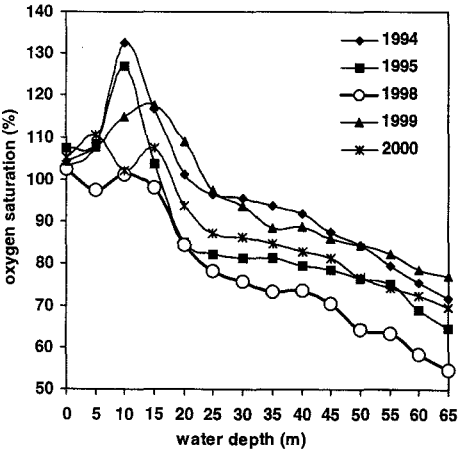

Fig. 9. Oxygen saturation (%) in Lake Stechlin at the end of the stratified periods in 1994, 1995, 1998, 1999 and 2000. Data represent average of 3 samplings between the end of August and the end of September.

permopsis raciborskii may occur in both deep and shallow lakes in the tropical region while it occurs exclusively in eu- to hypertrophic shallow lakes in the temperate region (PADISÁK 1997). When dealing with the evolutionary ecology of *C. raciborskii*, just its low photoadaptational parameter (I_k = 20 µmol m^{-2} s^{-1}) seemed to be paradoxical since prior to this study this species had not been found in deep layers of tropical lakes (PADISÁK 1997). After finding *C. raciborskii* in the DCM of a tropical lake we have a second example for what is known for *Planktothrix agardhii* or the *P. agardhii/rubescens* species complex: the same species may be a quite successful competitor in rather contrasting habitats. In this respect it is interesting to note that in some lakes, like Lake Balaton, *Cylindrospermopsis* and *Planktothrix agardhii* are strong competitors in late summer succession and the outcome of the competition depends on two factors: 1) low summer temperatures may prevent mass-germination of *Cylindrospermopsis* and therefore it cannot appear in large amounts, and 2) if low temperature does not prevent *Cylindrospermopsis* germination the actual N/P loading ratios are of importance. In the case of low N/P, *Cylindrospermopsis* will win due to its ability to fix atmospheric N_2, and if N/P is high *Planktothrix* is the likely winner. Such competition in deep layers of temperate lakes cannot occur since temperatures of 6–7°C in the upper hypolimnia are very likely to prevent successful competition of *C. raciborskii* because of its tropical origin.

Causes that led to the appearance and intensive growth of *Planktothrix rubescens* in Lake Stechlin remain unknown. Consequences on the lake's ecosystem are easier to assess. The quite large *Planktothrix* population was evenly distributed in the water column prior to stratification of the lake in May 1998. Then, a part of the population formed a DCM and continued growth and another part remained and sank slowly into the hypolimnion. Filaments were neither grazed nor decomposed therefore accumulated in the bottom region. Most of the P-pool of the lake remained "arrested" in this sinking population. The *Planktothrix* filaments certainly could not photosynthesize in lack of light however their respiration continued. This

led to a much higher hypolimnetic oxygen deficit at the end of the stratified period than occurred in the lake in other years (Fig. 9). According to microscopic observations, numbers of the ciliate *Stentor* with its symbiont *Chlorella*-like cells was much higher than in other years, however, exact investigations have not been carried out.

Development of deep population maxima of cyanoprokaryotes is probably much more wide-spread than it is known since such maxima may develop in any deep lake where $z_{eu} > z_{mix}$ and the ecological consequences of the DCM have been largely unexplored. They may cause important changes to the overall status of the lake by interferring with nutrient levels, matter and energy flow between trophic level, oxygen status of the hyplolimnia, etc. A future task is required to explore the ecology of dense upper-hypolimnetic phytoplankton populations which could present an important loop between epilimnetic and hypolimnetic communities by enhancing exchange of materials or just the opposite: the DCM could act as a kind of trap that prevents these exchange processes.

Acknowledgements

We thank Mrs Monika Papke, Mrs Elke Mach, Mrs Johanna Dalchow and Mrs Uta Mallok for their careful technical assistance in APP counting and chemical measurements.

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